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Functional relationships between soil organisms

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Summary :

Some aspects of the interactive roles of the soil microflora and fauna are generally reviewed, particularly as they occur in decomposing plant debris and in the root regions of higher plants. Examples, drawn from both microcosm and field studies, are given on the effects of grazing on the microflora and on the transmission of microbial inoculum by the soil fauna. The implications of these interactions on total soil biological activity, organic matter decomposition and nutrient release are considered.

Interactions of root pathogens, mycorrhizal fungi and soil fauna are briefly outlined. The implications of these interactions to primary production are considered.

Key words : soil microflora, soil fauna, mycorrhizae, microcosms, roots.

I. Introduction

It is accepted that the soil, with its surface layer(s) of decomposing plant debris and being permeated by the root systems of the vegetation it supports, represents a complex bio-physiochemical system supporting a large variety of organisms (microbes and fauna). Because of the heterogeneous distribution of organic matter, the microbes are (in the main) similarly distributed *i.e.* the soil represents a mosaic of microsites for microbial development.

Over the last few decades much data have been obtained on the population dynamics of members of the soil fauna (many of which have rather complex life histories), however we do not have such precise information on members of the soil microflora. Indeed, for any particular soil, no one would have the temerity to assert that the complete species complement of microorganisms was known or that, notwithstanding current interest, the relative importance of individual taxa in soil processes, their growth rates, turnover rates and extent of growth could be defined with any precision.

Despite these problems, various detailed studies on below ground biotas have been made and have generally indicated the large diversity of microbial taxa and a high microbial biomass in comparison with faunal groups. These initial descriptions (qualitative and quantitative) form essential starting points for ecosystem description and the understanding of energy and nutrient flows in the complex trophic level in soil/litter systems.

Furthermore, such detailed studies should form an essential starting-point in planning experimental studies on the functional relationships between specific groups of soil organisms.

From the body of data assembled it appears that the fungi, because of their biological attributes (HARLEY, 1971), are the important primary colonizers of freshly fallen plant debris. With increasing fragmentation and solubilization, the bacteria increase in importance. Faunal activities, through comminution of organic matter change in the physical environment to soil, change in substrate quality of organic debris during passage through the gut (*i.e.* chemical quality of faeces), grazing (selective or otherwise) on components of the microflora (*i.e.* their biomass and their metabolic activity), and the transmission of microbial inoculum through the litter system,

have important effects on energy and nutrient transfers. These effects appear to be much more important than might be expected, given that the fauna normally represent only a small proportion of the below-ground biomass.

The activities of the soil/litter biota are greatly influenced by both abiotic and biotic variables. Moisture availability and temperature differentially affect different groups of soil organisms. Substrate quality (chemical and physical) of available organic material is a well-known factor affecting patterns and rates of utilization as is the capability of decomposer organisms to concentrate nutrients during their feeding activities. The range of synergistic and antagonistic interactions between soil organisms must have profound effects on overall organic matter decomposition rates and nutrient cycling, these interactions range through antibiosis (including allelopathy, bacteriostasis, mycostasis), commensalism, parasitism and predation, competition and enhancement (with symbioses being the most striking example) (MIGNOLET, 1972). Phenomena such as predation, competition and enhancement (particularly symbioses) have been considered as the major ones affecting organic matter decomposition and nutrient cycling.

From the foregoing it must be apparent that within the soil/litter system a complex web of functional relationships exists within and between the groups of organisms present. The following discussion can only be a cursory (idiosyncratic) account of a small number of these relationships — in no way can it be considered even a partial review of this subject.

II. The litter layers

A great deal of attention has centered on the so-called succession of fungi on decomposing leaf litter on the soil surface. The detailed studies on this subject were summarized in DICKINSON & PUGH (1974) and were reviewed by HAYES (1979). The large body of data now available shows a successional scheme (GARRETT, 1963; HUDSON, 1968; HAYES, 1979) with parasites giving way to primary saprophytes (simple carbon compound utilizers) and then to secondary saprophytes (cellulose and lignin utilizers) plus secondary saprophytic sugar fungi. At all stages of the decomposition sequence, microorganisms capable of degrading microbial cells will be active. During the fungal colonization and degradation of plant debris nutrients are concentrated in the hyphae (CROMACK *et al.*, 1975), which may then be consumed by members of the litter fauna or die and be decomposed by bacteria and other fungi. Apart from the interactions between litter fauna and soil microorganisms, there are also inter-microbe interactions in litter layers (DICKINSON *et al.*, 1981).

As stated earlier, fungal activity in the layers of decomposing leaves will be determined by moisture and temperature conditions — conditions which will also affect the

location and activity of the variety of faunal groups (litter grazers, fungivores, detritivores and predators) in the litter layers. The interactive roles of the litter microflora and fauna in decomposition processes were reviewed by SATCHELL (1974) and he reiterated the view that soil invertebrate biomass acts « as a reservoir of plant nutrients » and acts as a brake to nutrient leaching from decomposing litter. This implies considerable consumption of microbial tissue (the primary decomposer organisms) by invertebrates. However data on this from various locations appears variable *i.e.* MITCHELL & PARKINSON (1976) found that oribatid mites consumed only 2 % of the fungal standing crop per year in a cool temperate forest soil, whereas McBRAYER *et al.* (1974) estimated, using a carbon flux model for a mesic hardwood soil, that 86 % of the fungal net production was consumed by fungivores. In an experimental attack on this problem COLEMAN & McGINNIS (1970) found that only 0.2 % of fungus placed in the field was eaten by animals. Nevertheless, the chemical quality of fungal hyphae (*i.e.* nitrogen content) has been shown to affect collembolan growth rates and reproduction (BOOTH & ANDERSON, 1979).

The passage of substantial amounts of plant and microbial material through the guts of litter invertebrates leads to the extrusion of such « processed » material as faeces in which the chemical quality and the microbial inoculum may be changed from that of the originally ingested material. Some of these faeces (e.g. mite faeces in the H layer of coniferous forest soils) may be resistant to decay and may represent a considerable nutrient pool. Recently studies on microorganisms in arthropod faeces has indicated that for *Oniscus asellus* feeding in sewage there was an increase in bacterial and nematode biomass and respiration after sewage was eaten and ejected as faeces (BROWN *et al.*, 1978). Working with *O. asellus* and *Glomeris marginata* (Villers), HANLON (1981) found that passage of leaf material through the animal guts led to a very considerable increase in bacterial standing crops (a period of increase which may be very short-lived) whereas fungal standing crops were decreased. BEHAN & HILL (1978) noted that on plating faecal pellets from seven oribatid mite species, fungi were isolated from only 14 % of the pellets.

The demonstration of selective feeding by the soil/litter fauna (at least in certain phases of their life histories) added a new dimension to this aspect of soil biology. Examination of gut contents and faeces of various soil fauna from a cool temperate woodland, together with conventional food preference studies for these organisms (MITCHELL & PARKINSON, 1976; DASH & CRAGG, 1972; VISSER & WHITTAKER, 1977; *n.b.* many other food preference studies for invertebrates from other sites have been omitted here), indicated that Enchytraeideae, Collembola, Acarina, Nematoda and insect larvae found pigmented fungi (e.g. *Ceuthospora* spp., *Cladosporium* spp., sterile dark forms) preferable to *Penicillium* spp. and *Paecilomyces* spp. Fortunately, a detailed knowledge of the fungi present (plus their frequency of occurrence) in the litter layers of this soil enabled the food preference studies to have at least some degree of reality. In a specific study (PARKINSON *et al.*, 1979) based on observa-

tions on fungal species and biomass changes during the spring thaw period (VISSER & PARKINSON, 1975), it was demonstrated in simple laboratory microcosms that selective grazing by a species of Collembola (*Onychiurus subtenuis*) on a sterile dark fungus could enhance the colonization of L-layer leaf by a basidiomycete. It was also apparent that the basidiomycete produced a volatile substance lethal to the Collembola and that, from observations of the effects of Collembola in sterile L-layer litter, the animals tracked considerable viable microbial inoculum into the litter.

SATCHELL (1974) reviewed the propositions (ENGELMANN, 1961; WALLWORK, 1967) that mycophagy stimulates the production of fungal mycelium, and concluded that the opposite could be true. HANLON & ANDERSON (1979) studied the effects of various grazing densities of *Folsomia candida* on *Coriolus versicolor* growing on macerated oak litter and a bacteria in the oak litter (their presence being a result of inadequate sterilization of litter and/or transmission by the animals). In the absence of any animals there was an increase in the standing crop of both bacteria and fungi over the experimental period, with a low number of animals (5 per experimental unit) there was an increase in oxygen uptake of the system, but with increasing density there was a decrease in oxygen uptake, a decrease in fungal standing crop and an increase in bacterial standing crop.

Thus, not only can selective grazing by Collembola affect interspecific competition for substrate colonization by important fungi in litter systems (PARKINSON *et al.*, 1979), but also under high levels of grazing pressure fungal growth is depressed and bacterial development is enhanced.

In a subsequent study, HANLON & ANDERSON (1980) showed that under optimal grazing densities macroarthropods (woodlice and millipedes) significantly enhanced microbial respiration (mixed microflora growing on oak leaf macerate). Enhancement of bacterial numbers, oxygen uptake and organic matter losses were demonstrated in sewage sludge as a result of adding rhabditid nematodes to systems containing bacterial inoculum (ABRAMS & MITCHELL, 1980).

VISSER *et al.* (1981), in a study of the effect of collembolan grazing on a sterile dark fungus growing on leaf litter, obtained data on system respiration which indicated an increase in respiration of the fungus following 10 days grazing. However these data were interpreted (on the basis of experimental data) as being the result of the growth of other microorganisms introduced into the experimental systems by the Collembola *i.e.* removal of the mycelium of the sterile dark fungus by grazing left cleared areas which were colonized by bacteria and/or fungi carried as contaminants by the experimental animals.

Over recent years, following observations of increased nutrient leaching from leaves grazed by millipedes (PATTEN & WITKAMP, 1967), various workers have posed the question « ***how does grazing by various groups of the soil fauna on the soil microflora affect nutrient release into the soil solution*** ».

The sequence of studies by COLEMAN and his colleagues on the effects of nematode and amoebal grazing on bacterial biomass, respiration and nutrient mineralization are examples of the microcosm approach to answering this question. COLEMAN *et al.* (1977) demonstrated that microfloral grazers (nematodes and amoebae with a pseudomonad) lead to a decrease in bacterial numbers and enhanced mineralization of nitrogen and phosphorus. COLE *et al.* (1978) working with the same group of organisms in simulated rhizosphere systems reported that the bacteria quickly assimilated much of the available inorganic phosphorus, but that much of this phosphorus was mineralized and returned to the inorganic phosphorus pool by amoebae. They found no mineralization of nitrogen or phosphorus in some of their experiments with nematodes (over 24 day experimental periods) despite decreased bacterial numbers and increased CO_2 evolution. In further experiments, ANDERSON *et al.* (1981), working on the effects of two species of bacterial grazing nematodes with a pseudomonad, showed that after 10 days there was an increased rate of glucose utilization and of nitrogen and phosphorus mineralization; but, after 65 days levels of soluble carbon, inorganic phosphorus and ammonium-nitrogen were similar in grazed and ungrazed systems. The bacterial grazers were reported to lead to increased CO_2 evolution together with a decline in bacterial numbers *i.e.* an accelerated turnover rate of the bacterial population was inferred.

VISSER *et al.* (1981) working on the effects of collembolan (*Onychiurus subtenuis*) grazing on a sterile dark fungus grown on L-layer leaf material reported that over a 10 day experimental period this had no significant effects on nitrate and phosphate leachability from the simple systems they were using. However INESON *et al.* (1983), working over a 12 week period on the effects of grazing by the collembolan *Folsomia candida* on a mixed microflora on oak leaf litter, recorded significant increases in the leaching of ammonium, nitrate and calcium as a consequence of grazing by the Collembola. They attribute the difference between their data and those of VISSER *et al.* (1981) to the different time period of the studies.

The foregoing examples all represent the use of very simplified microcosm approaches to the functional interactions between different groups of the soil biota. ANDERSON & INESON (1983) have pointed out that such laboratory experiments may be difficult to interpret in terms of actual field situations because of the extreme oversimplification involved in their design. Obviously, if there is an attempt to relate microcosm experiments to actual field phenomena, then their design (*i.e.* organisms used, their biomass, the temperature and moisture conditions and time course of experimentation) should have real relevance to the field conditions. Thus in the study by VISSER *et al.* (1981) it would have been artificial to have simulated anything more than a 10 day active grazing period, because at the time of year when the key organisms were active there was also a rapid drying of the L-layer litter which would drive the Collembola into lower litter layers.

In a more complex, long term (18 months) microcosm study BÅÅTH *et al.* (1981), a higher nitrogen mineralization rate was observed in the presence of animals which feed on bacteria — an observation which corresponds with the observations of COLEMAN *et al.* (1977). However no significant differences were observed in pine seedling growth or in nitrogen content of seedlings in microcosms with or without microbe-grazing fauna.

Field experiments on the effects of soil animals on microbial respiration have been relatively few. SATCHELL (1974) reviewed the field attempts, up to that time, to estimate the quantitative role of invertebrates in litter decomposition (e.g. exclusion and selective inhibition studies). He pointed out the hazards of some of these experiments and also that conflicting data have been obtained, particularly from studies where napthalene or dieldrin had been used to eliminate soil invertebrates from study areas.

More recently field studies (STANDEN, 1978; ADDISON & PARKINSON, 1978) have demonstrated increased microbial respiration when animals were present in experimental systems (fine mesh letter bags or soil cores) as compared with defaunated systems. Another approach to studying microbe-fauna interactions in organic matter processing is that by LUSSENHOP (1981). In this study of undisturbed, raked and burned prairie soil he found that increased plant productivity (as a result of burning) accelerated the degradation of plant material by fungi and oribatid mites, and that physical disturbance of the soil by raking increased bacterial activity (in degrading plant material and hyphae) and microarthropod density — it being hypothesized that this animal activity favoured bacterial over fungal growth. This type of detailed study followed by careful interpretation helps to place some of the « simple systems » into ecosystem perspective.

The role of animals as dispersal agents of fungal inoculum has been long known (see INGOLD, 1971). Undoubtedly most work has dealt with the role (frequently specialized) of insects as above-ground vectors of plant pathogenic fungi (e.g. conidia of *Claviceps purpurea*, pycniospores of rust fungi, brand spores of *Ustilago succisae*, Dutch elm disease, *Stereum congumoleutum*), with the spread of « cultivated » fungi by ants and ambrosia beetles, and with the casual above-ground spread of both pathogenic and saprophytic fungi.

With respect to studies on the role of the soil fauna in transmission of fungal inoculum in the litter/soil system, it was demonstrated by JACOT (1930) that oribatid mites carried fungal propagules on their bodies and various workers hypothesized on the possible importance of this. Recently, BEHAN & HILL (1978) isolated fungi occurring on several species of oribatid mites collected from various arctic and subarctic sites. They found that 60 % of the animals studied (347 mites) were carrying fungi. Identification of the fungi indicated 20 species being transmitted by the animals,

these fungi included three *Aspergillus* species and ten *Penicillium* species *i.e.* taxa which have not been considered as preferred food by the mites (MITCHELL & PARKINSON, 1976) but which are considered to have localized growth on organic debris on which sporulation will occur.

PHERSON & BEATTIE (1979) studied a range of invertebrates from beech leaf litter and found that Collembola appeared to carry the greatest number of fungal taxa per animal (averaging 0.5 to 2.2 taxa per animal with some animals carrying up to 4 genera). In their study 20 species of fungi from 9 genera were isolated from the invertebrates. They suggest that since, in the beech woodlands under study, maximum invertebrate activity coincides with bursts of fungal growth, faunal transmission of fungal inoculum could be critical for the inoculation of leaf material.

In a detailed study, attempting to assess the importance of transmission of fungal inoculum by Collembola on litter decomposition rates, VISSER & HASSALL (in prep.) sampled replicate cores of the litter horizon of a *Populus tremuloides* woodland. The cores were immediately separated into L, F_1, F_2 and H-layers and one collembolan species (*Onychiurus subtenuis*) was extracted (by hand sorting) from each replicate sample of each layer. In total 105 animals from each of the four litter layers were studied, each was (separately) placed onto a nutrient agar plate, allowed to move about the plate for 24 hours and then squashed into the agar. Microbial growth on the plate was recorded and fungi developing on the plates were identified. Bacteria were isolated from 98.8 % of the animals, and 94.3 % of the animals were carrying (or contained) viable fungal propagules. In all 130 species of fungi were isolated from the animals. Animals isolated from the L-layer averaged 3.9 propagules (from 3 species) per animal whilst those from the H-layer averaged 2.3 propagules (from 1.7 species) per animal. As might be expected from knowledge of the fungi present in the litter layers, *Mortierella* spp. (particularly *alpina* and *elongata*), *Cladosporium* spp. (particularly *raistrickii* and *syriacum*) were the most frequently isolated taxa together with *Beauveria bassiana*. It is interesting to note that various species never before isolated from this site were found on the collembola.

HASSALL (in prep.) has demonstrated the movement of *O. subtenuis* up and down the litter « profile » in response to changing moisture conditions — a phenomenon documented for other animal taxa in other ecosystems (e.g. SPRINGETT *et al.*, 1970; METZ, 1971; TAKEDA, 1978; WHITFORD *et al.*, 1981). Therefore it is interesting to speculate that, in ecosystems exposed to pronounced wet-dry cycles, transmission of microbial inoculum (particularly to freshly fallen L-layer litter), could be an important role of the soil arthropods and consequently significantly affect both the pattern of microbial colonization and decomposition rate of plant debris.

III. The root region

The release of nutrients from decomposing plant debris by the combined activities of the soil/litter organisms, and the leaching of these nutrients in the rooting zone of the vegetation makes them available for uptake by plants roots. However, AUSMUS *et al.* (1976) have demonstrated that in soil there is substantial immobilization of nutrients by the microflora *i.e.* there is potentially high competition between soil microorganisms and plant roots for available nutrients (a competition which could be affected by faunal grazing on the microflora).

The root region is known as a zone of intensified microbial activity and biomass where competitive and synergistic reactions between the roots and microorganisms (pathogenic and saprophytic) are greater than in the soil distant from the roots. Until recently the only faunal group to receive consistent study in the root region was the plant pathogenic nematodes.

Considerable attention has been given to the possible competition between root pathogenic and saprophytic fungi in rhizospheres (BAKER & COOK, 1974), an attention born out of interest to develop methods of biological control of the pathogens. However in this section only the interactions between plant pathogenic fungi and mycorrhizal associations and between soil fauna and mycorrhizae will be considered. It will be realized that many other types of functional relationships will exist between organisms in root regions.

Studies on interactions between mycorrhizal and non-symbiotic fungi in root regions have concentrated on studies of the effect of the symbioses on root pathogenic fungi. ZAK (1964) suggested that mycorrhizae could have a role in protecting roots against pathogenic attack (by efficiently utilizing available labile carbon compounds, by acting as a physical barrier, by secreting antibiotics, and by favouring protective rhizosphere organisms). MARX (1972) gave several examples of such root protection by ectomycorrhizal fungi against pathogens such as *Phytophtora cinnamoni* and *Rhizoctonia solani*, and of various mycorrhizal fungi being capable of inhibiting a substantial number of pathogens (some by antibiotic production). With respect to the interactions between VA mycorrhizal fungi and fungal root pathogens, no generalization can be made. In some cases VA mycorrhizae can predispose a host to infection, in other cases they can decrease susceptibility of the host to attack, in some cases they lessen the effects of the pathogen, and, in some cases they have no effects on disease development. SCHENK (1981) considered that, because VA mycorrhizae do not form a mantle or produce antibiotics, the mechanisms of protection (where it occurs) must be different from those of ectomycorrhizae. Thickened cell walls of V_A mycorrhizal plants and their biochemical states have been suggested as possible defence mechanisms.

Interactions between VA mycorrhizae and plant pathogenic nematodes have been studied since the early 1970's, and here again no generalizations can be made. O'BANNON & NEMEC (1979) quoted the major works done to that date and pointed out that variations in the host response to VA mycorrhizae and nematodes is complex *i.e.* in some cases disease symptoms are less severe in the presence of mycorrhizae, in other cases both mycorrhizal fungi and nematodes are adversely affected (through antagonistic reactions), and in other cases the mycorrhizae predispose the host to the effects of the pathogen.

The presence in the root region of fungus feeding members of the soil fauna might be expected potentially to have considerable impacts on mycorrhizal development. ZAK (1965, 1967) observed aphids and a nematode species feeding on mycorrhizae of Douglas fir, but experimental work on the implications of these associations was done by SUTHERLAND & FORTIN (1968) and RIFFLE (1969). SUTHERLAND & FORTIN (1968) reported that *Aphelenchus avenae* suppressed the growth of 6 species of ectomycorrhizal fungi in pure culture, but *Rhizopogon roseolus* did not allow good reproduction of the nematodes and appeared to produce a toxin against the animals. Further, they demonstrated in mycorrhizal synthesis studies (*Pinus resinosa* and *Suillus granulatus*) that *A. avenae* caused significant reduction in the formation of mycorrhizae.

SHAFER *et al.* (1981) pointed out that while some attention had been paid to the effects of fungus feeding nematodes on root disease fungi, little had been given to the effects of this group of nematodes on mycorrhizal fungi. Using pure cultures of five ericoid mycorrhizal fungi growing on nutrient agar plates with and without *Aphelenchoides bicaudatus* (286 ± 33 larvae and adults per plate), they found that nematode action caused destruction of aerial hyphae and severely limited lateral spread of hyphae of all species. If this phenomenon occurred under field conditions there could be severe limitation of endomycorrhizal development (and consequent limitation of nutrient uptake by ericoid roots).

The recent work of WARNOCK *et al.* (1982) on the effects of a collembolan on the VA mycorrhizal association in leek showed that in sterile sand pot cultures with and without *Glomus fasciculatus* and with and without *Folsomia candida*, plant weight of both mycorrhizal and non-mycorrhizal plants was reduced by the presence of the Collembola (with the mycorrhizal plants being most affected). The phosphate content of mycorrhizal plants grown with Collembola was particularly low, although there appeared to be no effects of the Collembola on the extent of mycorrhizal infection (although the authors emphasize that their data represent % root length infected, which gives no data on infection density). After 12 weeks there were approximately 3 times as many Collembola in the mycorrhizal systems as in non-mycorrhizal systems. Based on gut content studies, it was considered that the Collembola fed on *G. fasciculatus* and therefore reduced the effectiveness of the mycorrhiza.

Apart from the role of some soil fauna as grazers on mycorrhizal fungi, others may act as efficient vectors of these fungi. MACER *et al.* (1978) showed that in consuming sporophores of a variety of hypogeous mycorrhizal fungi (both ecto- and VA mycorrhizal forms) and ejecting viable spores of the fungi in faeces, small mammals could be important transmitters of mycorrhizal inoculum. Undoubtedly members of the soil invertebrate fauna will act in the transmission of mycorrhizal spores as they do for the spores of saprophyte soil/litter fungi.

From the fragmentary evidence available it is apparent that the soil fauna could, at least in certain situations, significantly affect the rates and degrees of mycorrhizal formation. Thus deleterious, indirect impacts on primary production could be achieved.

It would seem that more microcosm studies (well-designed) on mycorrhiza-fauna interactions (*cf.*WARNOCK *et al.*, 1982) could provide valuable information on the implications of faunal activity in root regions. However, in comparison with our knowledge of the litter decomposing fungi, we have few data on the general ecology of most mycorrhizal fungi *i.e.* their inoculum density, substrate relationships outside the root region, growth rates, competitive abilities in soil, etc.). An added problem is the fact that various mycorrhizal fungi cannot be grown in pure culture. Nevertheless the recent surge of interest in the mycorrhizal associations and their importance in nutrient uptake by plant roots should provide the basic data to allow experimental microcosm studies to be made with some degree of relevance to field situations.

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